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THE DISPUTED STRUCTURES OF THE MESONACIDÆ AND THEIR SIGNIFICANCE

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ABSTRACT

The disputed generic distinctions between *Olenellus*, *Mesonacis* and *Pædeumias* are examined. *Olenellus* and *Pædeumias* have similar structures posterior to the fifteenth segment of the thorax. Moreover, both genera have glabellas which do not reach the anterior margin of the cephalon while neither of them has uniformly developed intergenal spines. *Pædeumias* and *Olenellus* are, therefore, identical. The name *Olenellus* is retained through precedence, but Walcott's description of *Pædeumias* is the correct one for this fossil. *Mesonacis* differs from *Olenellus* in that it has a glabella which reaches the anterior margin of the cephalon and also in its possession of pleuræ on the rudimentary axial segments. Several species supposedly of *Olenellus*, whose pygidia and posterior segments of the thorax are unknown, belong in reality to the genus *Mesonacis*.

The Mesonacidæ possess facial sutures that are imperfectly fused, the remnants of which are seen on a few specimens of *Olenellus*, where their true course may be observed. These sutures, being of an advanced Opisthoparian type, indicate that this family belongs unquestionably to the order Opisthoparia.

The different adaptive features of both adult and young indicate that the Mesonacidæ were highly specialized, benthonic types which died out in the Lower Cambrian. The manner in which specialization occurs in this family indicates that the development of the different genera proceeded according to Raymond's theory, namely, that segments increase in number at the expense of the pygidium during evolution and do not become fewer as those scientists maintain who look to an annelid ancestry for the trilobites. As an example, *Mesonacis* is descended from *Olenellus* and is not ancestral to it. The Mesonacidæ exemplify an end stage in trilobite evolution and in no way disclose the origin of this subclass of crustaceans.

INTRODUCTION

The family Mesonacidæ is considered by most palæontologists to belong to the order Opisthoparia, Raw (1925, p. 311) and Swinnerton (1919, p. 110) being exceptions. It is described in the Eastman edition of Zittel's "Textbook of Palæontology" (1913, p. 692) as: "Opisthoparia with large cephalon and small and simple pygidium. Facial sutures in a state of symphysis and not to be distinguished. Eyes large, the palpebral lobes extending to the glabella. Glabella narrow, sometimes tapering towards the front. Thorax of numerous segments (thirteen to twenty-seven)." It should be added that these trilobites were benthonic crawling types and occasional burrowers in the mud (Raymond, 1920*b*, p. 101).

The Mesonacidæ are among the earliest known trilobites. They are confined to the Lower Cambrian, where they are the most numerous of this subclass of crustaceans. This family has certain peculiar structures that have led scientists to arrive at contradicting conclusions concerning the origin and development not only of the Mesonacidæ, but also of the whole subclass Trilobita. It is in order to determine clearly these disputed structures and to expose their true significance that this paper is written.

It is not the purpose of this article to describe in detail the different genera and species of the Mesonacidæ, but rather to clarify some of the disputed structures and theories of development of this family as a whole. In order to discuss intelligently their evolution and ontogeny, their principal structures should be carefully studied and, if possible, firmly established. Considering all that has hitherto been written about them and inferred from them, this task is quite sufficient for the present without delving into detailed classifications. Indeed, a revision of the genera *Nevadia*, *Callavia*, *Holmia*, and *Elliplocephala* and their respective species is undoubtedly needed. An examination of Walcott's[1] figures leads one to conclude that many of them are doubtful in their appearance, since it is not known how much the specimens have been touched up.

MATERIAL

In studying the Mesonacidæ the writer has had at his constant disposal specimens of *Pædeumias transitans*, *Olenellus thompsoni*, and *Wanneria walcottanus* from Pennsylvania and Vermont. These trilobites constitute three accessions in the department of Invertebrate Palæ-

[1]See Walcott, 1910, Pl. XXIII, Figs. 1, 4, 7; Pl. XXIV (complete); Pl. XXV (complete); Pl. XXVIII, Figs. 4, 8; Pl. XXIX (complete); also, Pl. XXIII, Fig. 5; Pl. XXIV, Figs. 3, 4, 6, 7.

ontology of the American Museum of Natural History. The writer has also examined specimens from Vermont in the Columbia University collection and some of the specimens from different parts of North America at the National Museum in Washington, D. C. He has also

Fig. 1

Fig. 2

Fig. 1. Mold of *Olenellus thompsoni* (×1.5), Lower Cambrian, Pennsylvania, showing the rudimentary segments of the thorax to the left of the spine on the fifteenth segment.

The facial sutures may also be recognized although they are considerably distorted due to the compression of this fossil. Both sutures extend from a point near the anterior end of the eyes to the margin of the cephalon. The suture on the left side of the glabella cuts the border at a point two-thirds of the distance from the genal angle to the anterior margin of the cephalon. The suture on the right side of the glabella is bent back from distortion so as to intersect the border at a point only one-third of the distance from the genal angle to the anterior margin of the cephalon. American Museum of Natural History. Accession 153.

Fig. 2. Mold of *Olenellus thompsoni* (×1.5), Lower Cambrian, Pennsylvania, showing the facial sutures.

The spine on the fifteenth segment of the thorax extends posteriorly in a straight line and so conceals the posterior rudimentary segments. American Museum of Natural History. Accession 160.

examined specimens from Vermont and Virginia, as well as some very well preserved ones that were collected in the summer of 1929, from Alberta, now in the Museum of Comparative Zoölogy at Harvard University. The trilobites from Jasper Park in Canada are in many

cases in an excellent state of preservation and exhibit features that are rarely preserved on mesonacid trilobites from other localities.

The bulk of the American Museum specimens which the writer has studied in detail are from the Lower Cambrian of Pennsylvania. These are contained in two accessions that were purchased in 1911, the one from I.S. and S.S. Simmons, and the other from Professor Atreus Wanner. The precise locality from which these fossils were collected is unknown. However, it is certain that it was somewhere in the Lancaster quadrangle (Lancaster County, Pa.), at or near the Fruitville quarry or at Noah Getz' quarry near Rohrerstown. The Simmons collection came from the beds at the base of the Kinzers formation of the Lower Cambrian, which has been described as follows: "Fossiliferous earthy blue dolomite, weathering to buff or orange-colored tripoli with hard brown skin; . . . . 7 [feet]" (Jonas and Stose, 1930, p. 28). The Wanner collection comes from the dark shales that overlie the earthy blue dolomite near the base of the Kinzers formation (Ibid.). There are but two species in both collections, *Pædeumias transitans* and *Wanneria walcottanus*. Approximately half the fossils have only the cephalon preserved. In the Wanner collection all the specimens are carefully numbered and listed, while in the other about one hundred have been arranged in a study series, being sufficiently well preserved to enable the student to draw conclusions therefrom.

Fig. 3. Mold of *Olenellus thompsoni* (×1.5), Lower Cambrian, Pennsylvania, showing the facial sutures and also the spine on the fifteenth segment of the thorax pushed to one side by the posterior rudimentary segments. A small remnant of these segments may be discerned to the left of the spine. American Museum of Natural History. Accession 160.

In addition to these two accessions there is one in the James Hall collection of 1870, which consists of about a dozen specimens of *Olenellus thompsoni* from the Lower Cambrian of Vermont. These are dark sericitic shales on which the trilobites are usually but imperfectly preserved. The general outlines are fairly complete, but the detail embodying such structures as eyelobes, appendages, spines, etc., are in most cases blurred and impossible to distinguish accurately. One specimen, however, is very well preserved in nearly all its detail. This trilobite is especially interesting as it was sketched and described by Whitfield

in 1884. This fossil has been photographed by the writer and is herewith given in figure 4.

The writer wishes to thank Dr. Chester A. Reeds, Dr. Percy E. Raymond, and Dr. J. J. Galloway for the invaluable assistance which they rendered on different occasions, and which enabled this paper to be written. Also, thanks are due to Dr. Charles P. Berkey and Dr. H. N. Coryell for their timely suggestions.

OLENELLUS, MESONACIS, AND *PÆDEUMIAS*

One of the most disputed features of the Mesonacidæ is the structure of *Olenellus, Mesonacis,* and *Pædeumias,* and consequently their respective delimitation and classification. *Olenellus* was first described by Hall as *Olenus* (Hall, 1859). It was later redescribed by him as *Barrandia* (Hall, 1860). Finally, when he discovered that the latter name was to be employed for another fossil before his own description would be published, he had it changed to *Olenellus* (Hall, 1862). It was later revised by Whitfield in 1884, who sketched a specimen which has been photographed and included in this paper. This specimen is, therefore, the first of the type specimens originally described to become reproduced later in an untouched photograph.

When Hall first described *Olenellus,* he ascribed two species to this genus—*thompsoni* and *vermontana* (Hall, 1859, 1860). The former has remained the genotype to this day, but the latter was found by Walcott in 1885 to merit being placed under a new genus. He named it *Mesonacis* and described *Mesonacis vermontana* as the type species, which it has remained ever since.

Finally, in 1910, Walcott described a new genus and species, *Pædeumias transitans.* He had been studying specimens from Pennsylvania, that were supposed to be *Olenellus thompsoni,* when he discovered that many of them had from two to six rudimentary segments and a small plate-like pygidium posterior to the spine-bearing fifteenth segment of the thorax. This feature differed so markedly from the pygidium, or rather the telson of *Olenellus* (Ibid., p. 312), as he had formerly described it, that he felt that these fossils belonged to a different genus.

Both before and, especially, since, the discovery of *Pædeumias,* the structure of the posterior portion of *Olenellus* has been keenly disputed. Walcott believed the pygidium of this fossil to be a long telson much like that seen in the modern horseshoe crab, *Limulus polyphemus.* This view, however, has since been discarded by Resser (1928, p. 5), Raw (1927, p. 137), and Raymond (1920*b*, p. 100). Resser merely

states his belief that *Olenellus* has a *Pædeumias*-like structure posterior to the fifteenth segment of the thorax, while Raymond reaches the same conclusion as the result of a zoölogical interpretation of trilobite structure. Raw regards *Olenellus* as merely having lost the rudimentary segments seen in *Pædeumias*, having reached one stage further than the latter in the evolution of the Mesonacidæ, as he interprets it. However, none of these writers has discussed this feature from the viewpoint of a graphic examination of observed structure, and their considerations of the biological interpretations are sufficiently brief to warrant further investigation.

In most specimens of *Pædeumias* the rudimentary segments are poorly preserved compared with the rest of the trilobite. They may be seen on the specimen in figure 1 where they appear to be very delicate as compared with the other structures. It should be noted that the spine on the fifteenth segment of the thorax appears to have been pushed out of the normal position by these segments. This feature was apparently regarded by Walcott as a means of identifying this fossil when the rudimentary segments were not preserved. Some of his figured specimens show this type very clearly (Walcott, 1910, Pl. XXXIV, Figs. 1, 2, 3, 9). However, when this spine was not pushed aside it frequently covered up these segments when the animal was buried in the mud, and so *Pædeumias* became indistinguishable from a supposedly telson-bearing *Olenellus*. The specimens in figures 2 and 4 show this feature. Furthermore, when the trilobite is poorly preserved throughout, which is the case with most of the specimens from Vermont, the rudimentary segments of the thorax and the small plate-like pygidium, the structures most easily destroyed, may become blurred and confused with the axial spine, which thus appears remarkably broad at the anterior end and tapers posteriorly, thereby acquiring also a striking resemblance to a typical *Limulus*-like telson. Indeed when the rudimentary segments are observable there can be no question about the pygidium. Unfortunately, however, this is rarely the case. In fact, these segments were discovered but comparatively recently and were first described only in 1910 by Walcott (p. 304). Since *Olenellus* had been known as long ago as 1859, it is not surprising that this fossil should have been considered as having a terminal telson, especially when specimens like that in figure 4 were studied. We have seen that the rudimentary segments of the thorax and pygidium of *Pædeumias* have been clearly shown to exist, but that, on the other hand, there is nothing in the appearance of the fossil to indicate with certainty the existence of the telson-like pygidium of

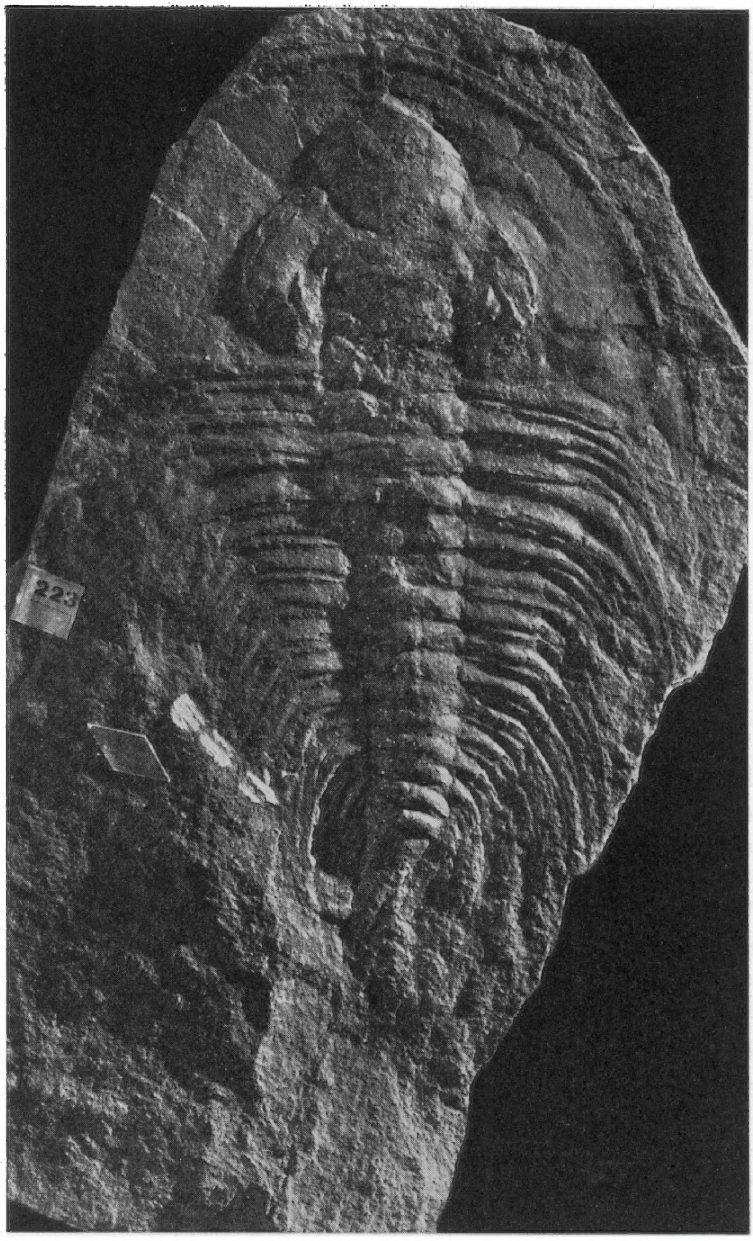

Fig. 4. Mold of *Olenellus thompsoni* (natural size), Lower Cambrian, Vermont.

This specimen was found in Parker's quarry, Georgia, Vermont, and is one of the best specimens known. It was described and figured by R. P. Whitfield in 1884 and is the earliest of the described specimens to be reproduced in an untouched photograph. American Museum of Natural History. Catalogue No. 223.

Olenellus. A biological interpretation must, therefore, be looked to as the only alternative to indicate the existence of the latter structure, and so it is to this aspect of the discussion that we must now turn.

The principal proponents for a telson for *Olenellus* are Walcott and Swinnerton. Swinnerton (1923, p. 247) explains that the telson is found in the most primitive trilobites, and that new segments are formed from tissue produced at its anterior margin. The pygidium is then found only when these segments are not separated from each other as quickly as they are produced. He gives *Nevadia* as a typical example of the primitive trilobite with a telson. In so doing he has gone further than any other writer, including Walcott, who thus described this fossil: "Pygidium apparently a continuation of the axial lobe without pleural lobes or spines; it is a small and, as far as can be determined from compressed specimens, it is a simple plate of about equal length and breadth that narrows toward the posterior margin" (Walcott, 1910, p. 259). An examination of this fossil in figure 14 shows no change in the structure of the axial portion except at the posterior end where a small plate-like pygidium may be seen (Ibid., p. 257). However, if this theory about the pygidium of trilobites holds for this fossil, its origin and development are altogether different from that given by Walcott, who, describing the *Olenellus* stage in the development of the Mesonacidæ, states: ". . . the fifteenth segment a strong terminal telson; posterior rudimentary segments and true pygidium of the *Pædeumias* stage absorbed or the rudimentary segments and pygidium have disappeared and the large median spine of *Pædeumias* has become the telson of *Olenellus*." (Ibid., p. 245.)

We now have two contradictory theories for the existence of the telson in trilobites. According to Swinnerton the telson is a primary structure and the pygidium a secondary one, whereas according to Walcott it is precisely the reverse. Swinnerton does not explain the existence of the telson beyond implying that it should exist due to its similarity to the structure of the annelid whence trilobites are supposed to have been descended. He appears merely to have postulated its existence in order to explain the development of trilobites. So little evidence of the existence of a telson as Swinnerton offers must be rejected until he has presented some more substantial proof. Walcott's theory, on the other hand, appears to have been postulated in order to explain a structure which has been shown to possess a very deceptive appearance. That there is nothing in the appearance of the pygidium of *Olenellus* to lead one to regard it as a telson places the burden of proof on Walcott's explanation of its existence. Concerning that explanation Raymond

exclaimed: "This would mean the cutting off of the anus and the posterior part of the alimentary canal and developing a new anal opening on the spine of one of the thoracic segments!" (Raymond, 1920*b*, p. 101). Since the theories of Walcott and Swinnerton lack substantial evidence, and are unsupported by other writers, they cannot be accepted.

The only other writer to draw distinction between *Olenellus* and *Pædeumias*, according to differences of pygidial structure, is Raw. He regards *Olenellus* as an end form in the evolution of the Mesonacidæ, which had lost all of the rudimentary segments in *Pædeumias*. (Raw, 1927, p. 146). According to him the difference between these two fossils is purely theoretical. Since it has been shown that the rudimentary segments and pygidium of this fossil are easily destroyed and become often confused with the spine on the fifteenth segment of the thorax, there can be no way of knowing that they did not once exist. His distinction is, therefore, too impracticable for purposes either of identification or of classification, especially since this fossil is usually destroyed posterior to the fifteenth segment of the thorax. The developmental aspect of Raw's theory will be dealt with in detail further on. These two genera must, therefore, be regarded as possessing identical structures posterior to the fifteenth segment of the thorax so that distinctions between them must be looked for in other parts of the body.

Differences in the cephalon between *Olenellus* and *Pædeumias* were mentioned by Walcott (1910, p. 338), and were later summarized and dealt with in greater detail by Resser who classified these two genera along with *Mesonacis* according to their distinctions in this structure (Resser, 1928, p. 5). Resser considers that *Olenellus* and *Pædeumias* differ only in the cephalon, while *Olenellus* and *Mesonacis*, similar in the cephalon, differ chiefly in the posterior segments of the thorax and pygidium. It is, therefore, evident that according to his classification *Pædeumias* and *Mesonacis* must differ in both cephalon and pygidium. It should be mentioned that Resser accepts Walcott's description of the posterior portions of *Mesonacis* and *of Pædeumias*, and that the description of the latter genus applies as well for *Olenellus*.

According to Resser the cephalon of *Pædeumias* is characterized by intergenal spines and by a glabella which fails to reach the anterior border of the cephalon, as contrasted with the cephalon of *Mesonacis* and *Olenellus* in which there are no intergenal spines and in which the glabella touches the anterior border. According to him the only way in which *Olenellus* differs from *Mesonacis* in the cephalon is by the greater length of the eyes and by a doubtfully wider rim (Ibid.).

In the writer's collection there is great variation in the development of intergenal spines. Many of them, as in figures 2 and 4, lack intergenal spines and, at the same time, have a glabella which does not reach the anterior margin of the cephalon. This feature alone eliminates intergenal spines as a factor of importance in classification.

In pointing out differences in the forward extension of the glabella, Resser has contributed a most valuable means of distinguishing *Mesonacis* from *Pædeumias*. However, according to this classification *Olenellus* remains ambiguous. The breadth of the cephalon affords no criterion for distinction, especially since the rim of the type specimen of *Mesonacis gilberti* is as broad as that of any specimen of *Olenellus* or *Pædeumias* (Walcott, 1916, pp. 406, 412). Moreover, the eyes are approximately as long as those on either of these fossils. Resser points out that Walcott's rendering of *Olenellus thompsoni* is based not upon Hall's original figures but upon an incorrect restoration of a very poorly preserved specimen (Resser, 1928, p. 4). He goes on to state: "This figure, as Walcott stated in 1910 (description of Pl. xxxv, Fig. 1), is incorrect in representing the anterior lobe of the glabella as not reaching the rim" (Ibid.). Indeed, Walcott stated that the glabella of this fossil had been crushed down even with the surface of the cheeks so that its termination at the border was not observable (Ibid., p. 404). However, it is doubtful whether it would have reached the border even had it not been crushed.

Walcott referred to Hall's original figure of *Olenus thompsoni* as showing the anterior lobe of the glabella terminating in front at the marginal border (Ibid., p. 338). An examination of this figure shows the eyes and the glabella so completely destroyed that one cannot determine their exact position on the cephalon (Hall, 1859, p. 60, Fig. 1). The following year Hall redescribed this fossil as *Barrandia thompsoni* along with *Barrandia vermontana* which was later renamed *Mesonacis vermontana* by Walcott (1885, p. 328). This second description of Hall's is much more detailed and complete than his first one, of which he stated at the time he wrote it that it was only superficial and needed to be revised (Hall, 1859, p. 59). He figures *O. thompsoni* with the glabella not reaching the anterior border, as contrasted with that in *O. vermontana*, in which it decidedly does reach the border (Hall, 1860, pp. 116, 117). The authority of Hall's writings would, therefore, indicate that, contrary to the opinion of Walcott and Resser, the anterior lobe of the glabella in *Olenellus* did not reach the anterior border of the cephalon but was separated therefrom by a distinct space.

Indeed, Walcott states that he found many well-preserved specimens on which the anterior lobe of the glabella reached the anterior border (Walcott, 1910, p. 338). However, he does not say whether they were entire specimens or whether the pygidium was preserved. In fact, none of these specimens has been figured by either Walcott or Resser, and, until they have been figured, there is no reason to suppose that they may not be specimens of *Mesonacis*. On the other hand, the specimen which was sent to the American Museum from the type locality (Parker's quarry, Georgia, Vt.), and which Whitfield described in 1884, is extremely well preserved and has been recently photographed[1] by the writer. Indeed, Resser might regard this fossil as a specimen of *Pædeumias*, but, until one with the features of *Olenellus*, as he describes them, has been clearly shown to exist, this specimen, along with Hall's, deserves to continue to be called *Olenellus* as it was originally described. Inasmuch as neither Walcott nor Resser has shown that *Olenellus* has a cephalon like that of *Mesonacis*, and unlike that of *Pædeumias*, and since the original descriptions of Hall and Whitfield do indicate that the cephalons of *Olenellus* and *Pædeumias* are alike, these two genera must be regarded as having similar cephalons.

Thus the pygidium and cephalon of *Olenellus* and of *Pædeumias* are alike. Inasmuch as there are no other disputed differences between them, these two genera must be regarded as identical. The name *Olenellus* should be retained by virtue of precedence, but Walcott's description of *Pædeumias* is the correct one for this fossil.

It should also be pointed out that the species *robsonensis* really belongs to the genus *Mesonacis* and not to *Pædeumias*. Burling assigned this fossil to the genus *Pædeumias* because of its resemblance to *Olenellus gilberti* in all respects other than the number of rudimentary segments. However, since Walcott discovered that the latter species belonged to the genus *Mesonacis*, objections to placing the species *robsonensis* in the same genus have been removed. Moreover, the species *robsonensis* has rudimentary segments typical of *Mesonacis* in that it has pleural as well as axial segments. It differs from *M. gilberti* and *M. vermontana* only in that it has a greater number of them (Burling, 1916, p. 57, Pl. 1). Furthermore, according to Resser's classification, this fossil has a glabella typical of *Mesonacis* in that it reaches the anterior margin of the cephalon.

[1]See Fig. 4; also Whitfield, 1884, p. 151 and Pl. xv, Fig. 1. Due to the well-preserved condition of this specimen and to the fact that it is the most anciently described specimen to be reproduced in an untouched photograph, it should be regarded as the most important plesiotype of *Olenellus* at the present time.

It should also be mentioned that Resser renamed, described, and figured *Olenellus fremonti* as *Mesonacis fremonti*, and in addition described *Mesonacis insolens* and *Mesonacis bristolensis* (Resser, 1928). From what has been observed about the glabella of *Mesonacis*, the species *canadensis*, *claytoni* and *argentus* belong also to this genus.[1]

THE FACIAL SUTURE

Another disputed feature of the Mesonacidæ concerns itself with the existence of facial sutures. Mr. Frank Raw has recently revived this subject in his papers: "The Development of *Leptoplastus salteri* and other trilobites" (Raw, 1925), and "The Ontogenies of trilobites and their significance" (Raw, 1927). In both of these papers he deals largely with the general head plan of trilobites as determined by their cephalic spines. He furthermore shows the forward and backward revolution of the facial sutures of certain trilobites by the complementary migration of the cephalic spines. With regard to the Mesonacidæ he attempts to show that the facial sutures along with the cephalic spines have revolved backwards. However, before explaining this phenomenon he briefly outlines the history concerning the sutures of this family. Due to its extreme importance his summary will be herewith reproduced (Raw, 1925, p. 301).

Whitfield (1884) was the first to describe the course of the facial sutures of *Olenellus* on a Vermont specimen of *Olenellus thompsoni*. Walcott, however, rejected the former's description, stating that the sutures Whitfield described were but accidental breaks (Walcott, 1886, p. 163). Walcott then proceeded to describe the course of facial sutures on *Olenellus* (*Mesonacis*) *gilberti* as follows: "The facial suture cuts the anterior margin some distance outside the line of the outer margin of the glabella and passes obliquely inward to the anterior angle of the eye lobe; curving around the outer margin of this, it passes obliquely outward to the posterior margin, cutting it midway between the glabellar lobe and the outer margin of the genal angle." (Ibid., p. 172.) He also stated that "What I had identified as the facial suture is a raised line in the cast of the interior of the shell that fills a depressed line occupying the position of the suture." (Walcott, 1891, p. 633.) He later redescribed the posterior portion of the suture as passing from the back of the eye to the intergenal angle and being sometimes continued into a short spine (Walcott, 1910, p. 327). However, he goes on to contradict

[1]See Walcott, 1910, p. 410, Pl. xxxviii, Fig. 1; p. 415, Pl. xl, Figs. 10, 11, 14, 15.

his former description of the anterior portion of the suture, stating: "No traces of facial sutures have been observed in front of the eye" (Ibid.).

Raw accepts Walcott's final description of the posterior portion of the facial suture and likewise his view as to the absence of the anterior portion. He then proceeds to develop the unique theory briefly referred to above. After assuming the comparative shortening of the cephalon during growth and observing the absence of the procranidials in the adults, he attempts to show that the three pairs of cephalic spines moved downward and inward during the growth of the trilobite. He considers that the metacranidials became crowded and finally aborted, their place being taken by the encroaching parials, while the procranidials moved posteriorly to assume the position once held by the parials. He goes further to insist that the anterior portion of the facial sutures revolved back to the genal angles along with the procranidial spines, stating: "If, however, it be accepted that the genal spines of the Mesonacids are procranidials, the backward course of the suture is inevitable, for these must terminate behind (and so within) the procranidial spines." (Raw, 1925, p. 303).

Raw (1927, p. 142) arrived at the foregoing conclusions after studying Walcott's (1910, p. 305) description of *Pædeumias transitans* and has drawn his figures after Walcott (1910, Pls. XXXII and XXXIV) to illustrate his theory. His interpretation of the evolution of the trilobite from the stage represented by figure 22 to that represented by figure 23 is very doubtful, since the backward and inward revolution of the spines appears to be postulated rather than actually observed. On the other hand, it appears far more probable, according to Raw's own sketch, that the spines A and B in figure 23 (except that they are rather more developed) are the same as those represented by B and C on figure 22.

Commenting on Raw's second article, Raymond (1928, p. 168) pointed out that the parial and metacranidial spines necessarily had to move outward and not inward during the process of growth and that the metacranidials atrophied as the parials became functional. Raymond based his explanation on the ontogeny of trilobites as described by Beecher. This explains clearly the significance of the metacranidials since it shows that they protect the trilobite during the protaspis stage when the transverse structure dividing the pygidium from the cephalon first appears. It is only later that the free cheeks appear with their spines, the parials (Ibid.). These spines move outward with increase in width of the cephalon (Ibid.). Such a development was described and figured

by Walcott (1910, p. 326; also Pl. XXV), as Swinnerton pointed out after Raw's first paper was read. (Raw, 1925, p. 322). Swinnerton further stated that the examples Raw gave were too few to be of phylogenetic importance, even with regard to the Mesonacidæ (Ibid.). Both Swinnerton and Raymond regard these spines as due merely to larval adaptation (Ibid., also Raymond, 1928, p. 168). Swinnerton has also clearly shown the danger of attaching too much significance to the embryonic structures of trilobites (Swinnerton, 1919, p. 108). Inasmuch as there are apparent flaws in both the theoretical and observational aspects of Raw's theory, and since the majority of other writers have since regarded his view unfavorably, his entire theory must be regarded as improbable.

On the other hand, in the writer's collection one out of every fifteen specimens shows a pronounced line extending obliquely outward and forward from a point about four-fifths of the distance from the rear to the front end of the eye lobe, to the margin of the cephalon. This may clearly be seen in figures 1, 2, and 3. A similar phenomenon has been observed by the writer on specimens which were collected in Jasper Park, Alberta, by the Harvard Summer School expedition of 1929. One of these specimens not only displays the feature described above but also shows very clearly the posterior portion of the facial suture as Walcott (1886, p. 164) described it,—a feature not seen on the American Museum specimens. Inasmuch as so many of these trilobites show lines all similarly located in front of the eye, it appears only reasonable that these lines are at least the course followed by the original suture, if not the actual suture itself. These lines may conform to what Walcott (1891, p. 633) once described as a raised line in the cast of the interior of the shell that fills a depressed line occupying the position of the suture. However, they do not occur in the same place on the cephalon either as those described by Hall (1860, p. 116) and later by Whitfield (1884, Pl. XV), or as those described by Walcott (1886, Pl. XX; also 1891, Pl. LXXXVI). The course of the facial suture as described and figured by the first two writers is a great deal closer to the glabella, while the one described and figured by Walcott is also further forward and inward than the course of the sutures in the American Museum specimens. The fact that these writers had identified the wrong lines may have led Walcott later to deny the existence of the anterior portion of the facial sutures,—the view that has since been held by most writers.

An exception is to be found in the opinion of Professor Raymond (1917, p. 206), who identified the cracks on specimens figured by Walcott (1910, Pls. XXV, XXVI, XXVII, XLII) as traces of facial sutures. On the

first of the figures to which he refers (*Elliptocephala asaphoides*), cracks may be seen on a distorted specimen (Pl. XXIV, Fig. 5), which more or less correspond to those on the specimens in the American Museum collection. On Plates XXVI and XXVII, however, these cracks do not appear on any of the figured specimens. But on Plate XXII the figure of a specimen of *Callavia callavei* shows these cracks very distinctly, located in the same position on the cephalon as those on the American Museum specimens. It is a curious fact that somewhat later, Raw (1925, p. 303), commenting on Raymond's observation, stated: "Raymond, 1917, p. 206, was misled by a faked photograph supplied by me (Walcott, 1910, p. 418, and Pl. XLII, fig. 1) into identifying a crack across the specimen as the anterior branch of the suture." Indeed, this figure does not look altogether natural, but it seems probable that the cracks Raymond referred to are genuine and that what he saw are the true sutures or their traces in spite of Raw's alterations.

With the course of the facial suture in the Mesonacidæ now established, Raw's theory concerning their backward revolution is impossible. Moreover, if what he states about the essential relationship of the sutures to the cephalic spines be accepted, the backward migration of the latter becomes likewise impossible. Furthermore, it may now be stated with certainty that this family of trilobites can belong only to the order Opisthoparia, of which they are typical representatives in every respect, except that their facial sutures are secondarily fused.

GENERAL DISCUSSION

The structure of the cephalon, the number of segments in the thorax, the pygidium, and the mode of life to which they were adapted, have led many writers to arrive at different conclusions concerning the origin and development not only of the Mesonacidæ but of all other trilobites as well. In writing about *Pædeumias robsonensis*, Burling (1916, p. 53) began his paper with the remark: "By common consent we are accustomed to regard the crustacea as derived from the annelids, and we have pointed to their abundantly segmented body as a reason for assigning this ancestorship to them." Raw (1927, p. 140) shows the gradual reduction of segments in a chart explaining the evolution of the Mesonacidæ from *Mesonacis* through *Pædeumias* to *Olenellus*. This view held by these writers is well summarized in Walcott's (1910, p. 249) statement: "The development of the Mesonacidæ from some annelidian-like ancestor by the gradual combination of segments to form the cephalon and pygidium is indicated by the examples cited of *Nevadia*, *Elliptocephala*, *Holmia*, and *Pædeumias*."

Opposed to this view is Raymond (1920*a*, p. 22), who looks to a primitive arthropod as ancestral to the trilobites. He pointed out that the growing point in trilobites, as in all other arthropods, is immediately in front of the anal segment and furthermore stated that the free segments of the thorax grow through degeneration of the pygidium. In fact the greatness of the pygidium appears to be inversely proportional to the number of segments in the thorax. As an example Raymond cites the relationship of *Dalmanites eucentrus* to *Dalmanites mucronatus*. The latter occurs in beds immediately beneath the former and differs from it only by having a larger pygidium. *Dalmanites eucentrus* has a pygidium of the same proportional dimensions (with the rest of the trilobite in the larval stages) as that of *Dalmanites mucronatus* and becomes reduced only in the adult stage (Ibid., p. 23). It is, therefore, obvious that Raymond considers that the Mesonacidæ and other trilobites with small pygidia and numerous segments in the thorax are advanced in the scale of trilobite evolution, in contrast with Walcott and others who regard them as primitive.

The most detailed arguments in behalf of an annelid ancestry for trilobites is perhaps to be found in the works of Swinnerton (1919, p. 109), who saw in the Mesonacidæ features that were characteristically primitive and favorable to his theory. These were: the presence of pleuræ in the cheek region of the larval forms, the absence of facial sutures, and the dorsal location of the eyes in both adult and young (Ibid.). The fact that the eyes were dorsally located in the Mesonacidæ when no facial suture was present, indicates that there was no connection between those two organs, and that neither—certainly not the eyes——had migrated back from the border during the course of evolution. However, the existence of facial sutures as well as their true course has now been demonstrated and, therefore, Swinnerton's contention is disproved, unless it can be shown that the eyes and sutures were primitive and in the habit of traveling in the opposite direction during evolution.

In order to test this theory properly, an examination of all trilobite orders, with the exception of the Hypoparia, should be made. Turning to Zittel's "Textbook of Palæontology" (1913, p. 712, Fig. 1364, and p. 723, Fig. 1398), one finds the sutures on the cephalons of representative Opisthoparia and Proparia graphically displayed (after Beecher). An inward migration of the eye and facial sutures may be observed in both orders as the geologic column is ascended. In the Opisthoparia, the sutures of *Atops* and *Conocoryphe* of the Lower and Middle Cambrian, respectively, are close to the border. In *Olenus* of

the Upper Cambrian and Ordovician, the sutures are found midway between the glabella and the border, while in Proëtus, ranging from the Ordovician to the Carboniferous, they are found close to the glabella. In the Proparia, the sutures of *Placoparia*, which is found only in the Ordovician, are close to the border; in *Cheirurus* and *Dalmanitina* of the Ordovician and Silurian, they have migrated about half way in; and in *Dalmanites*, closely related to the last-named genus but occurring later, and in *Phacops* and other Phacopidæ of the Devonian, the sutures have moved close to the glabella. In all cases, both in the Opisthoparia and in the Proparia, the facial sutures have borne the eyes and have migrated backward and inward during the course of evolution, a fact which indicates that Swinnerton's theory is highly improbable. It is furthermore evident that with regard to the facial sutures and the eyes, which appear to be highly developed, the Mesonacidæ are highly specialized and far advanced in the scale of evolution. Perhaps the most striking proof of the specialized condition of the mesonacid sutures is that the only other known example of fused sutures is to be found in *Phacops*, which is universally regarded as a very highly specialized trilobite and an end-product in the scale of evolution.

Since the sutures of the Mesonacidæ are advanced in position and development, their rudimentary or vestigial structure is due to specialization rather than to primitiveness. They are, therefore, in a state of symphysis, being in a process of secondary fusion.

Another structure in the cephalon that is often indicative of specialization is the glabella. Swinnerton (1919, p. 108) states: "Thus an increase in the width of the anterior segments of the glabella is frequently exhibited by the more advanced members of a progressive series, cf. *Olenellus* with *Nevadia*." This statement certainly holds for one line of evolution in the Mesonacidæ, namely, that from *Nevadia* to *Wanneria*. According to Walcott's (1910, p. 249) chart, *Callavia*, *Holmia*, and *Wanneria* have progressively larger glabellas than those of each preceding member of the series. However, according to this statement, *Mesonacis* should be descended from, instead of ancestral to, *Olenellus* as Walcott (Ibid.) and Raw (1927, p. 140) have considered it. Both of these writers show that in the line of descent in the Mesonacidæ, *Mesonacis* was followed by *Pædeumias* which was in turn followed by *Olenellus*. Their charts differ only in that Walcott inserts *Elliptocephala* as an intermediate member between *Mesonacis* and *Pædeumias*. Raw's placing of this genus prior to *Mesonacis*, instead of between it and *Pædeumias*, is undoubtedly an improvement, since *Elliptocephala* obviously differs

far too greatly from the other two to be considered an intermediate stage between them. (*Elliptocephala* has eighteen instead of fourteen segments in the thorax and also lacks the enlarged third segment of *Olenellus* and *Mesonacis*, and has altogether different posterior thoracic segments.) It has already been shown that the glabella of *Olenellus* does not reach the anterior border, whereas that of *Mesonacis* not only touches it but, in the case of *M. vermontana*, *M. fremonti*, *M. canadensis*, *M. claytoni*, and *M. argentus*, is broadened anteriorly and pushes it forward. It should be noted that with the exception of *M. vermontana* all of the above species were placed as members of the genus *Olenellus* by Walcott but have since been shown according to Resser's classification to belong to the genus *Mesonacis*. It is, therefore, only since the papers of Raw and Walcott appeared that the delimitation of *Olenellus* and *Mesonacis* in the glabella was clearly understood—thanks to Resser's classification. According to Swinnerton, *Mesonacis* followed *Olenellus* and did not precede it. The fact that the glabella in certain species of *Mesonacis* pushes the anterior margin forward is an additional specialization that is not seen in *Olenellus*, which, therefore, further confirms Swinnerton's view.

Let us consider *Mesonacis robsonensis*—probably the most extraordinary trilobite ever discovered. As in all other species of *Mesonacis*, the cephalon contains eyes and facial sutures that are specialized in structure and in position, according to Beecher's classification of the Opisthoparia. It has also a glabella that is even more specialized than that of the closely related genus *Olenellus*. Along with genal and, perhaps, remnants of intergenal spines, these features indicate that the cephalon is highly specialized in every way. The anterior fifteen segments of the thorax with its third member enlarged, all containing highly ridged and furrowed pleuræ with spines, along with the posterior twenty-nine or more rudimentary segments, a most unique structure among trilobites, appear distinctly specialized rather than primitive unless this species be closely related to the annelids. Considering the general anatomical aspects of this fossil, a highly specialized pygidium is more consistent with the specialized cephalon and thorax than would be a primitive one. This is especially true if it be borne in mind that if the pygidium were primitive it must have remained unchanged whilst the thorax and the cephalon became specialized.

Concerning the development of *Mesonacis robsonensis* as exemplifying the evolution of the Mesonacidæ from the annelids, Burling (1916, p. 55) states: "The finding of 29 rudimentary posterior segments would

seem to indicate that this resorption takes place laterally, that is, they become smaller in size before they become fewer in number." In other words, after these segments had retained their rudimentary nature whilst the remainder of the animal became specialized, they underwent a radical change, both horizontally and vertically, while the rest of the trilobite remained unchanged. The lateral resorption of segments is unlikely according to any annelid theory of trilobite evolution, since it implies a narrowing and consequently a relative lengthening of the body. Furthermore, no segments have fused to form a pygidium as Swinnerton's theory maintains.

If, on the other hand, it be supposed that the Mesonacidæ were not closely related to the annelids but were specialized trilobites evolved in the manner stated by Raymond (1920*a*, p. 22), virtually no difficulties are found either in accounting for their development in the environment they had, or in reconciling their different structures with one another. The multi-segmented thorax and small pygidium, along with the specialized facial sutures, eyes, and, in the case of *Wanneria* and *Mesonacis*, the glabella, are all in keeping with one another and with the idea that this family is distinctly specialized. Due to the fact that their structures are unique among trilobites, the rudimentary segments of *Olenellus* and *Mesonacis* may also be regarded as specialized structures, especially *M. robsonensis*, whose development casts an interesting reflection on the environment of the Mesonacidæ and its stimulating influences toward adaptation.

Raymond (1920*b*, p. 73) has pointed out that during Lower Cambrian times all trilobites, with the exception of the Agnostidæ and the Eodiscidæ, had small pygidia and were adapted only for crawling or floating. This state of affairs lasted throughout the Cambrian in the eastern portion of North America. However, in the Pacific seas three trilobite families with caudalized pygidia appeared in the Middle Cambrian, while another one appeared in the Upper Cambrian. In the Ordovician, caudalization reached a climax, and swimming types were developed all over the world, while the crawling ones with small pygidia disappeared. Raymond explains this change as due to the rise of predatory cephalopods and fishes, the natural enemies of trilobites, which, being initiated in the Pacific realm, rendered existence impossible except for the swimming forms.

Let us now consider the distribution of the Mesonacidæ. The only genera of this family that are well known and that are seen in great abundance in many parts of the world are *Mesonacis* and *Olenellus*. It

should herewith be mentioned that hardly any of the European members of this family are found in sufficient abundance to permit generalization. The most abundant and the best known types for this purpose are found only in North America. On this continent it is evident that *Mesonacis* predominated in the Pacific seas, whereas *Olenellus* did so in the Atlantic waters. *M. gilberti*, *M. claytoni*, *M. bristolensis*, *M. robsonensis*, *M. insolens*, *M. canadensis*, and *M. argentus*, are abundant in the west, whereas *M. vermontana*, the only eastern form of this genus, is rarely ever seen. In contrast with this genus, *Olenellus* is abundantly represented in the Lower Cambrian of eastern North America by *O. thompsoni*, whereas *O. truemani* and *O. logani*, the western species of this genus, are comparatively rare. We have already seen that in structure *Mesonacis* is further advanced from *Olenellus*. When it is remembered that straight cephalopods and other newcomers appeared first in the Pacific seas and further stimulated adaptation by their presence, it is not surprising that we should here find that *Mesonacis* rather than *Olenellus* was abundant; on the other hand, the latter was still the more abundant of the two in the quieter waters of the Atlantic. Indeed, the eccentric segments of *M. robsonensis* are not unlikely the result of unsuccessful caudalization, while the secondary fusion of the sutures may be an adaptation for burrowing.

Concerning this fossil, Burling (1916, p. 54) writes: "The fourth, fifth and sixth pleuræ on the right side of the specimen described have suffered injury, being broken off close to the axis at such a time or in such a manner that the ends have healed, and show a tendency toward normal termination. The fifth one in particular is broken clear across, and in it the pleural groove stops just inside of the newly curved margin; the fourth and sixth were broken across transversely so as to leave the greater portion respectively of the upper and lower margins. This particular trilobite is as large or larger than the largest that has so far been discovered in the Lower Cambrian of British Columbia or Alberta. If we assume that the accident occurred during the youth of the trilobite, we must grant that these early forms did not have the power of renewing broken or lost portions, but this conclusion is negatived by its ability to heal up the broken ends and fashion them off. The accident was, therefore, probably of recent occurrence. And since it must have happened during his maturity, we are somewhat justified in assuming that our trilobite lost this portion of his anatomy to a foe more voracious, if not larger, than himself. The occurrence certainly lends weight to the inference that the Lower Cambrian trilobite was not the supreme

arbiter we have supposed him to be; however,—he may have been struck by material dislodged from a ledge beneath which he was crawling."

As one would expect in the case of specialized animals, the Mesonacidæ probably left no descendants—certainly *Mesonacis* did not. Walcott considered that *Paradoxides* was descended from *Wanneria*. Indeed, this genus greatly resembles *Wanneria*, from which it differs only in being larger and in having a relatively larger and more specialized glabella, as well as usually more free segments in the thorax. The chief objection to this theory has been that *Paradoxides* with its well-defined facial suture could not have been descended from a mesonacid with its sutures secondarily fused. The difficulty of having to postulate the return of facial sutures in *Paradoxides* makes the descent of this fossil from the Mesonacidæ improbable. The relation of this genus to the Mesonacidæ is perhaps best explained as having been descended from a common ancestor (Raw, 1925, p. 309). It is also interesting to note that the specialized *Paradoxides* died out at the close of the Middle Cambrian and left no descendants.

Having seen that the Mesonacidæ were not closely related to the annelids, it now becomes apparent that their eccentric features, such as the fused sutures and the rudimentary segments of *Masonacis robsonensis*, are those of marked specialization. It is, therefore, remarkable that such an unusual type of trilobite as the Mesonacidæ should be found in the Lower Cambrian along with such dissimilar primitive forms as the Agnostidæ. However, this becomes easily understood when it is remembered that the former are end stages in the evolution of the benthonic types—soon to become extinguished—whereas the latter are primitive pelagic types that were destined to hold their own until the end of the Palæozoic era. The origin of the Mesonacidæ, therefore, becomes obscure and almost impossible to determine. Moreover, little can be learned from the study of their larval forms, since these, too, have specialized features—such as extra pairs of cephalic spines—that are not seen in the adults, but which are, nevertheless, merely features of adaptation (Raymond, 1928, p. 168; Raw, 1925, p. 322; Swinnerton, 1919, p. 109). Both Swinnerton (1919, p. 108) and Raymond (1928, p. 169) pointed out that no reliable conclusions could be arrived at from the study of the embryonic forms. It is for that reason that they have not been discussed in this paper.

It may indeed be true that the unusually eccentric and degenerate features of some of the more advanced genera of the Mesonacidæ in-

dicate an acceleration in the evolution of the animal kingdom brought about by the arrival of cephalopods and other new classes of animals. Specialization in the later benthonic trilobites does not appear to be so acute as in the Mesonacidæ, possibly indicating that the former merely had to compete with other animals that were already there but did not have to become adapted to a changing environment. Of course, this view is purely hypothetical and probably never can be satisfactorily proved. However, from what we have seen, it may be truly stated that both structural and developmental evidence show that the Mesonacidæ were highly specialized benthonic trilobites which afford no criterion indicating the evolution of arthropods from annelids, inasmuch as this family is far removed from any relationship with the latter.

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